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A CONTRIBUTION TOWARD A HISTORY OF THE ARCTIC MOSS FLORA

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INTRODUCTION

The existence of a unique group of bryophytes occurring largely in the circumarctic region north of the tree line was recognized by Steere (1953, 1965) who considered them to be representatives of a High Arctic Floristic Element. He postulated that the species had once belonged to a "widely distributed Tertiary flora now restricted to unglaciated arctic areas by continental glaciation at lower latitudes" (1969, p. 510).

I show here that some high-arctic mosses, together with other species of a more general far northern distribution, in fact were present in midcontinent North America at about 40° North Latitude as recently as 20,000 radiocarbon years ago (yr B.P.), i.e., at or several thousand years before the onset of retreat from the maximum position attained by the Wisconsinan Laurentide ice sheet. These full-glacial paleobryofloras are about 10,000 years older than the more completely documented late-glacial moss floras that existed in the Great Lakes–New England region at about 11,000 yr B.P. (Miller 1984). The glacial maximum floras indicate that open, tundralike vegetation prevailed when the fossils were buried. Species of both upland, well-drained sites and wetlands are represented. I suggest that these ancient southern occurrences of mosses of present arctic distribution were the result of dispersal rather than the remnants of the pre-Pleistocene flora. Thus midcontinent North America and regions to the east and west along the limit of continental glaciation may have been a center of dispersal for the arctic flora, joining unglaciated Beringia, parts of the Arctic Archipelago, and other northern refugia as potential source areas for plants migrating into the North American Arctic during the late Quaternary.

The phytogeography of mosses and hepatics has been an enduring topic of inquiry to which Howard Crum (1972), whom we honor in this Festschrift, and many others in North America (e.g., Schofield 1969; Schofield and Crum 1972; Steere 1965; Schuster 1983) have made significant contributions. This body of work has influenced the theory and practice of bryophyte systematics and investigations into the evolutionary biology of bryophytes. In most phytogeographical studies bryologists have emphasized the analysis and interpretation of existing distributional areas. However, attempts to trace the origins of floras have been weakened by the absence of information on the occurrence of species through time. This is mainly because there may be only a slight correspondence between the present and past distributions of a given species. But there is an excellent source of data about past distributions because the Quaternary fossil record of the mosses of glaciated regions is very rich, as studies by paleobotanists and paleoecologists have repeatedly demonstrated over the past two decades. Therefore, opportunities for new phytogeographical syntheses will result as the paleobotanical record is integrated with what is known about the distribution of the extant flora. I recommend that future phytogeographical studies be designed to gather original data about fossil mosses, and that existing data about fossil bryophytes be utilized in analyses of the patterns of distribution.

Fossil mosses are convenient subjects in studies of historical plant geography for several reasons. Isolated and cleaned of associated sediment, they can be dissected, sectioned, and mounted for examination under a microscope much as one would a fresh sample of moss plants. Preservation is sometimes incomplete, owing to degradation caused by one or a number of possible biological or physical processes, or cellular details may be obscured by the deposition of iron pyrite or other minerals. In general, however, fossils of mosses are easy to work with, and during the identification process one soon learns what diagnostic characters to evaluate against those of the reference specimens. Moreover, the Quaternary moss record appears to be characterized by little or no extinction, or at least no fossils of extinct species have yet been adequately documented. Procedures used in the study of Quaternary bryophyte fossils are summarized by Janssens (1990) and Miller (1990).

I report here on my continuing studies of moss fossils from Pleistocene deposits in Illinois, Ohio, and nearby regions that are associated with deposits marking the farthest extension of the late-Wisconsinan glaciation. This research has included analyses of other plant fossils, such as pollen and the remains of vascular plants, the results of which were obtained in collaboration with colleagues and will be presented more fully elsewhere. I briefly review these data to provide information on the paleoenvironmental settings of the floras. However, the emphasis of this paper is on phytogeography and in particular the history of the arctic moss flora.

SITE DESCRIPTIONS

The location of the fossil beds (FIG. 1), a short description of the stratigraphy at each of the sites, and radiocarbon dates pertinent to the age of moss fossils are given below.

1. Clinton Power Station Site, De Witt County, Illinois, 8 km east of Clinton. Buried moss peat was discovered during excavations resulting from the construction of a nuclear power station. The 1–2-cm-thick moss bed occurred beneath loess (1.5 m), tills of the Wedron Formation (9.4 m), and clay (0.1 m) (measurements from surface) and above 0.9 m of Morton loess. The age of the moss peat was 20,670 ± 280 yr. B.P. (ISGS-828). The stratigraphic information and samples of the peat were sent to me by James E. King, then of the Illinois State Museum, Springfield.

2. Sharonville Site, Hamilton County, Ohio, 1.5 km southeast of Sharonville. A 2–3-cm-thick layer of peat, interpreted as A_0 paleosol and marking the upper limit of a deposit of organic-rich silt of variable thickness (to 50 cm), is exposed along a tributary of Mill Creek for a distance of approximately 8 m. Above the organic bed is 0–40 cm of clay, and above this is compact diamicton (till). The geology of the site is described more completely by Lowell *et al.* (1990b). They report the age of the organic bed as 21,120 ± 130 yr. B.P. (PITT-0225) and also give 19,670 ± 68 yr. B.P. as the average of five age determinations of wood from a cluster of four tamarack stumps in growth position at the top of the organic silt. The average is taken as the age of the area when it was overriden by the continental ice margin. Mosses were extracted from a sample consisting of the peat and the sediments immediately

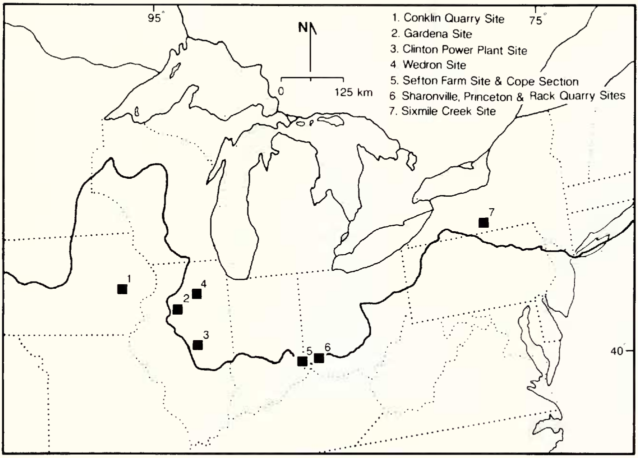

FIG. 1. Map of central and eastern North America showing location of full-glacial paleobotanical sites mentioned in text and approximate limit of Wisconsinan glaciation (dark line).

above and below (KS-87-09-AA). The sample was collected by Thomas Lowell and Kevin Savage, Department of Geology, University of Cincinnati.

3. Princeton Sewage Treatment Plant Site, Hamilton County, Ohio, 1 km northeast of Glendale. Excavations associated with expansion of the plant revealed a thin continuous peat bed over a deposit of organic silt, beneath (from top) diamicton (3 m) and a layer of silt (0.25 m), with discontinuous clay-rich zones in contact with the peat. Two samples from the southwest corner of the excavation (TL-87-214-AA and TL-87-214-CC) yielded the moss fossils reported here. From a third sample (TL-87-214-DD) a small twig, probably of willow (*Salix* sp.), was removed from the peat, cleaned, and dated, using accelerator mass spectrometry (AMS). Its age was 19,135 ± 160 yr. B.P. (Beta-34385, ETH-6063).

4. Rack Sand Quarry Site, Hamilton County, Ohio, 8 km north of the business center of Cincinnati. A peat bed, 0.4–0.5 m thick, exposed on the north wall of the quarry was sampled for pollen and bryophytes on my behalf during the summer of 1988 by Jerry Snider, Department of Biological Sciences, University of Cincinnati. The geology, paleobotany, and paleontology of the site are being investigated by Thomas Lowell, Kevin Savage, and other colleagues (Lowell *et al.* 1990a). The peat overlies a dense clay and is itself overlain by about 5 m of clay that contains silt interbeds and lenses. The upper 2–2.5 m of the topmost clay is oxidized, indicating that it is weathered. The radiocarbon age of a small twig from near the bottom of the peat was 20,230 ± 300 yr B.P. (Beta-33944, ETH-5951), and a second twig from the clay just above the peat was 19,060 ± 265 yr B.P. (Beta-33943, ETH-5950). These ages were obtained by the AMS method. A third age (Lowell *et al.* 1990a), obtained by conventional radiocarbon analysis of wood from the peat, was 19,470 ± 115 (PITT-0510).

METHODS

Sediment samples containing moss fossils were soaked in 5% Na_2CO_3 in beakers until the sediment disaggregated. Some samples required soaking for 14 hours or longer in warm (70°C) Na_2CO_3. The sediment chunks were gently pulled apart by hand to avoid degrading the fossils. Samples consisting of more than one type of sediment, for example, lower clay–peat–upper clay sequences, were separated into uniform subsamples that were treated separately. When the sediment had been reduced to a slurry, it was poured into a 250-μm-mesh sieve through which small particles then were washed with tapwater. Residues retained on the mesh were soaked in distilled water for 24 hours or until the water remained clear after standing for an hour or more, and then were examined microscopically. The fossils were sorted and identified, and stems and leaves were sectioned when necessary. A set of the fossils mounted in Hoyer's solution has been deposited in the Quaternary Paleobotany Collection of the New York State Museum.

RESULTS

To place each of the fossil moss assemblages in a paleoenvironmental context, results of pollen and plant macrofossils analysis are described and interpreted briefly.

Clinton. The pollen assemblage in the moss peat (counted by J. E. King) is dominated by pine and sedge pollen, the latter accounting for 62% of the total. Excluding sedge pollen (which presumably originated mostly from wetland plants growing in the depositional basin), pine (59%) and grass (18%) are the principal pollen types, with spruce (4%), birch (3%), willow (2%), and ragweed (7%) present in low amounts. Together, the six pollen types amount to 93% of the assemblage. These data and the low influx of total pollen (estimated at 821 grains/cm^2/yr under the assumption that the peat accumulated in 40 years; cf. radiocarbon dates and peat thickness for Rack) indicate that treeless landscapes occurred nearby under climatic conditions similar to those at places in the contemporary Arctic where low pollen influx has been registered.

Sharonville. Pollen counts by S. T. Jackson revealed a moderately high sedge total (18% when Cyperaceae were included in the percentage base). With sedges excluded the principal pollen types were spruce (41%), pine (36%), grass (8%), and Compositae (7%, including 1% ragweed). These account for 92% of the assemblage. Needles (spruce), wood (spruce, larch), and twigs (*Juniperus horizontalis*) are present in the moss peat. The pollen and macrofossils indicate an open landscape, with spruce and tamarack in scattered stands and interspersed open, dry or mesic sites in which light-demanding mosses and shrubs grew (Miller and Jackson 1989).

Princeton. The moss peat contained a higher percentage of sedge pollen (40% when Cyperaceae were included in the percentage base) than at Sharonville. Other components (with sedge pollen excluded from the calculations) were spruce (37%), pine (37%), grass (12%), *Thalictrum* (5%), and Compositae (3%, including 1% ragweed). Most (95%) of the pollen assemblage is distributed among these five categories. Small willow stems with buds and one spruce seed occurred in the moss peat, but no spruce needles were recovered; this contrasts with the Sharonville peat in which they were abundant. The similarities and contrasts between the Sharon-

TABLE 1. Composition of full-glacial moss floras represented in buried peats from sites in Illinois and Ohio (see text).

	Clinton	Sharonville	Princeton		Rack
			214-AA	214-CC	
Amblystegium serpens	.	.	.	X	.
Brachythecium turgidum	X	.	.	X	.
Bryum neodamense	X	.	.	.	X
B. pseudotriquetrum	X	.	X	X	X
B. sp[1]	.	X	.	.	.
Calliergon giganteum	X	.	.	.	X
Campylium chrysophyllum	.	X	X	X	.
C. stellatum	X	.	.	X	X
Cinclidium latifolium	X	.	.	.	.
C. stygium	.	.	.	.	X
Cratoneuron filicinum	.	.	X	X	.
Dicranella sp.	.	X	.	.	.
Didymodon asperifolius	.	.	X	X	.
Ditrichum flexicaule	.	.	X	X	.
Drepanocladus aduncus	X	.	.	.	.
D. brevifolius	.	.	X	.	.
D. revolvens	X	.	.	.	X
D. uncinatus	.	X	.	.	.
Hypnum lindbergii	X	.	.	.	.
Meesia triquetra	.	.	.	.	X
Polytrichum commune	X	.	.	.	.
Scorpidium scorpioides	.	.	.	.	X
Thuidium abietinum	.	X	X	X	.
Tortula norvegica	.	.	X	X	.
Totals	10	5	8	10	8

[1]A third but unidentifiable species of *Bryum*.

ville and Princeton records indicate that trees were absent or very sparse locally at Princeton (Miller and Jackson 1989), or if some were present, that conditions were not appropriate for preservation of their remains.

Rack. Seven stratigraphically separated samples from a 30 cm section of moss peat (sample interval 3–5 cm) yielded pollen assemblages dominated by sedge, spruce, and pine. Sedge representation varied from 17–48% ($\bar{x}$ = 37%), with Cyperaceae totals included in the percentage calculations. Data for other principal types (with sedge excluded from the percentage base) were spruce 42–56% ($\bar{x}$ = 47%), pine 29–42% ($\bar{x}$ = 35%), oak 1–4% ($\bar{x}$ = 2%), grass 3–8% ($\bar{x}$ = 4%), and Compositae 1–5% ($\bar{x}$ = 3%). These types accounted for over 90% of each pollen assemblage. Total pollen influx appears to have been very low, 400–1122 grains/cm^2/yr ($\bar{x}$ = 806) and similar to results obtained for the Clinton moss peat. The low pollen deposition rates at Clinton and Rack indicate an open, tundralike vegetation, with trees and other plants that produce abundant, well-dispersed pollen located at places distant from the moss beds.

Mosses. Samples of the peat beds at the four sites yielded plants of 24 species of mosses (TABLE 1). Most (16) were represented in only one of the fossil beds. Two mosses, *Bryum pseudotriquetrum* and *Campylium stellatum* were present at three of the four sites, but no moss was a member of all four assemblages. The sites contained fossils of five, eight, or 11 species.

The fossils were well preserved in all samples, and numerous fragments were

TABLE 2. Percent-composition of fossil moss assemblages in four samples of the peat bed at Rack Quarry, Hamilton County, Ohio.

species/sample number	1	2	3	4
Scorpidium scorpioides	35	30	35	30
Drepanocladus revolvens	35	25	30	30
Meesia triquetra	5	30	30	5
Campylium stellatum	20	–	–	25
Cinclidium stygium	t	5	t	5
Calliergon giganteum	5	–	t	5
Bryum neodamense	–	10	5	–
B. pseudotriquetum	t	–	–	–
Number of species	7	5	6	6

t = trace

recovered for most species. For the fossils that could be identified only to genus (*Bryum*, *Dicranella*), either sporophytes were absent or too little plant material was available to reveal diagnostic characteristics.

Replicate samples from Princeton (TABLE 1) and Rack (TABLE 2) were studied to compare the representation of species in the peats. The two samples from Princeton were 1 m apart and together yielded fossils of 11 mosses. Seven species were represented in both samples, and four were in one but not the other, with three unique to sample CC and one to AA. The four samples from Rack were from a 25 cm^2 area, and both species presence and values for percent composition were determined. For the latter a subsample was removed from each sample and sorted into components. A visual estimate of the area occupied by each component was taken, using centimeter graph paper. Fossils of eight species were present in the four samples, but no single sample had all eight. The totals varied from five to seven (TABLE 2). There was also considerable variation in the composition of the four assemblages, but the leading species were *Scorpidium scorpioides*, *Drepanocladus revolvens*, and *Meesia triquetra*. Five species were present in trace amounts or were absent from some of the subsamples.

DISCUSSION

Before beginning a phytogeographical analyses of fossil moss assemblages, it is useful to interpret and summarize the paleoenvironments existing at the time the fossils were deposited. The four moss beds appear to have been buried by silt and clay, with little or no predepositional transport of the fossils. The best evidence for this conclusion is that the species mixtures are comparable in composition to extant bryophyte communities. At Clinton and Rack the mosses are indicative of rich-fen peatland systems, which develop in association with standing calcareous ground water and are typically dominated by brown mosses. At Rack a rich fen existed for 1200 radiocarbon years under what appear to have been unvarying environmental conditions, as indicated by the more or less uniform pollen spectra across the 30-cm-stratigraphic interval. The deposition of clay from a lake, probably the result of a rise in the water table caused by glacier advance, buried the mosses at Clinton and Rack. In contrast the Princeton and Sharonville assemblages are dominated by mosses of upland, well-drained or mesic habitats, such as an area with microscale relief consisting of a mosaic of sites from the tops of soil mounds to less well-drained interswales and edaphically intermediate topography. At Sharonville the mosses appear to have been buried by silt or clay deposited from a lake; at Princeton perhaps by wind-blown silt (loess). The fossil assemblages at both places indicate *in situ* burial with little or no mixing of plants derived from substantially different contemporary moss communities, for example, those of wet versus dry habitats.

The full-glacial vegetation of parts of the North American Middle West, especially in Ohio where logs have been frequently found in late-Wisconsinan tills, has been interpreted as forest (Burns 1958; Goldthwait 1958; see also Wright 1981) or tree line tundra, with stands of trees and extensive open areas (Martin 1959). More recently, information has become available that strongly favors the latter interpretation. This includes the results of studies at Conklin Quarry (southeastern Iowa; Baker *et al.* 1986), Biggsville (northwestern Illinois; Baker *et al.* 1989), the Athens North Quarry and Gardena sites (central Illinois; F. King 1979; J. King 1979), and Wedron (northeastern Illinois; Garry *et al.* 1990), as well as data from the Clinton, Sharonville, Princeton, and Rack sites (Lowell *et al.* 1990a; Miller and Jackson 1989). When long records are available, for example at Biggsville and Athens North Quarry, there is evidence of a transition from spruce-pine forest (28,000–25,000 yr B.P.) to more open spruce-tamarack forest that lasted until 22,500 yr B.P. (Garry *et al.* 1990). This change was presumably in response to the gradual onset of glacial conditions, which culminated with the invasion of the continental ice margin circa 20,500 to 19,000 yr B.P. in the Illinois/Ohio region. Although evidence is scant for the time between 22,500 yr B.P. and the glacial maximum, available data indicate continued change toward more open landscapes such as those documented by fossils in the Clinton, Sharonville, Princeton, and Rack moss peats. Of these four records, only the Sharonville peat contains spruce needles and larch wood, indicating local presence of spruce and tamarack trees. Moss peats at the four sites contain mainly spruce, pine, and sedge pollen, but the influx values indicate distant sources for spruce and pine. The best working interpretation of the data now available is that full-glacial landscapes in midcontinent North America were open but that trees (spruce and tamarack) occurred at some places, producing together a pattern similar to that along the tree line in northern Canada where open tundra and stands of spruce and tamarack are intermingled.

Phytogeography. The four moss florules described here (Table 1) consist of species that are mostly broadly northern in distribution, with many now widespread in the northern United States (and sometimes southward in the mountains), through boreal Canada, and into the Subarctic and Arctic. Examples are *Cinclidium stygium* (Fig. 2; range mapped by Mogensen 1973) and *Meesia triquetra* (range mapped by Montagnes 1990). In contrast to the North American late-glacial moss flora (Miller 1976) few southern species appear to be represented in the full-glacial sites. An exception is *Campylium chrysophyllum,* which is distributed mainly in areas of deciduous forest or mixed conifer-deciduous forest, and which is recorded from Princeton.

Thirteen species in addition to the 24 mosses listed in Table 1 have been reported from the following full-glacial deposits in the central United States: Conklin Quarry, Iowa (Baker *et al.* 1986; Janssens and Baker 1984)—*Barbula fallax, Brachythecium reflexum, Distichium* cf. *capillaceum, Drepanocladus vernicosus, Hygrohypnum luridum,* and *Tomentypnum nitens;* Gardena, Illinois (J. King 1979; Miller 1979, with additions recorded here)—*Hypnum lindbergii, Plagiomnium medium* subsp. *curvatulum* (reported as *Mnium* (*Plagiomnium*) cf. *rugicum* by Miller 1979; revision by G. S. Mogensen), and *Scorpidium turgescens;* Wedron,

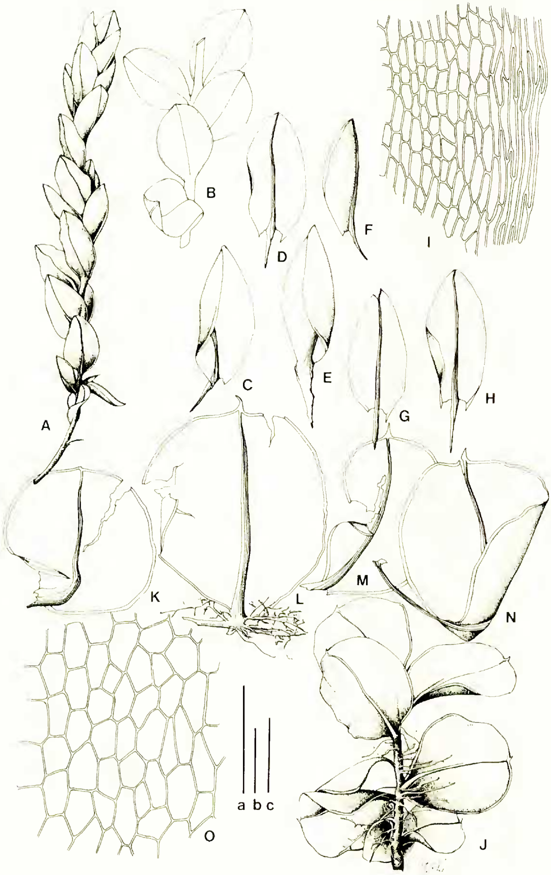

FIG. 2. Full-glacial fossil mosses from the Rack Quarry Site, Cincinnati, Ohio. A–I. *Bryum neodamense*. A. Habit (scale bar a). B. Portion of stem with leaves (a). C–H. Leaves showing short decurrencies (b). I. Cells at leaf margin (c). J–O. *Cinclidium stygium*. J. Habit (a). K–N. Leaves (b). O. Median laminal leaf cells (c). Scale bars: a = 3 mm, b = 1 mm, c = 100 μm. Drawings by Patricia M. Eckel.

Illinois (Garry *et al.* 1990)—*Hypnum pratense;* and Connorsville interstadial deposits at Sefton Farm and the Cope Section, Fayette and Franklin counties, Indiana, respectively [the age of wood from the Connorsville interstadial is 20,000 ± 500 yr B.P. (I-610); Kapp and Gooding 1964, p. 311]—*Bryum lisae* var. *cuspidatum* (as *B. cuspidatum*), *Campylium polygamum*, *Ceratodon purpureus*, and *Rhizomnium punctatum* (as *M. punctatum*).

Three of the full-glacial mosses, *Cinclidium latifolium* (Fig. 3), *Didymodon asperifolius,* and *Drepanocladus brevifolius,* are of special interest in connection with the history of the arctic moss flora. The North American distribution of *C. latifolium* is shown in Figure 4, and Schofield (1972) has mapped North American occurrences of the other two species. All three mosses are cited by Steere (1965) as belonging to the circumpolar arctic element, and the main part of their contemporary ranges is the High Arctic. A fourth species, *Bryum neodamense* Itz. (Fig. 2) may also belong to this distribution type. In North America it is generally treated as a synonym of *B. pseudotriquetrum* (Hedw.) Gaertn., Meyer & Scherb. but is kept separate from it in the European floras of Nyholm (1958), Smith (1978), and others. Little attention has been paid to *B. neodamense* by North American bryologists, and the few published records of its occurrence are from Ellesmere Island (Holmen 1953; Brassard 1971, 1976), arctic Alaska (Steere 1978), Devon Island (Canadian Arctic Archipelago; Vitt 1975), and Yukon Territory and Quebec (Ireland *et al.* 1987). Its broad, obtuse, strongly concave, short-decurrent leaves seem diagnostic (Fig. 2). Moreover, the fossils are green-brown, unlike the largely black ones of *B. pseudotriquetrum,* which have lanceolate, sometimes broad, long-decurrent leaves, and which I have recovered repeatedly from Pleistocene sediments. If the status of *B. neodamense* as a species withstands taxonomic scrutiny, it may turn out to be frequent in North America in high latitude rich fens and other calcareous hydric habitats. It seems, however, to be absent in the continental rich fens of Alberta and nearby areas (D. H. Vitt, pers. comm., 2 Oct. 1989).

Midcontinent North America (ca. 40° North Latitude), based on the evidence presented here, may have served as a late-Pleistocene center of dispersal for elements of the arctic flora. For this to have happened, northward dispersal would have had to kept pace with deglaciation and outpaced postglacial climatic warming and the development of forest communities. There is some direct (fossil) evidence that populations of arctic mosses were present in younger deposits north of the full-glacial sites described here. For example, Janssens (1984) discovered fossils of *Cinclidium latifolium* and *Drepanocladus brevifolius* in late-glacial sediments deposited between 16,000 and 11,000 yr B.P. in Kotiranta Lake, Carlton County, northeastern Minnesota. Other late-glacial occurrences of arctic mosses north of the full-glacial sites described here are cited in Miller (1984). Moreover, it seems likely that a search of late-glacial sediments in lakes in southern and boreal Canada would reveal additional and younger fossils of arctic mosses. If this turns out not to be the case, populations of arctic species in midcontinent North America perhaps became extirpated as a result of climatic and other environmental changes and did not disperse northward, as has been postulated for the arctic beetles that occurred in the same region during the Wisconsinan glacial maximum (Schwert and Ashworth 1988). Extirpation or disperal as contrasting hypotheses can be evaluated as more data are gathered at new study sites in northern North America.

There is some evidence that high-arctic mosses were present at midlatitudes in North America earlier in the Pleistocene just before the onset of full-glacial conditions. Analyses of a buried organic bed exposed along Sixmile Creek, south of

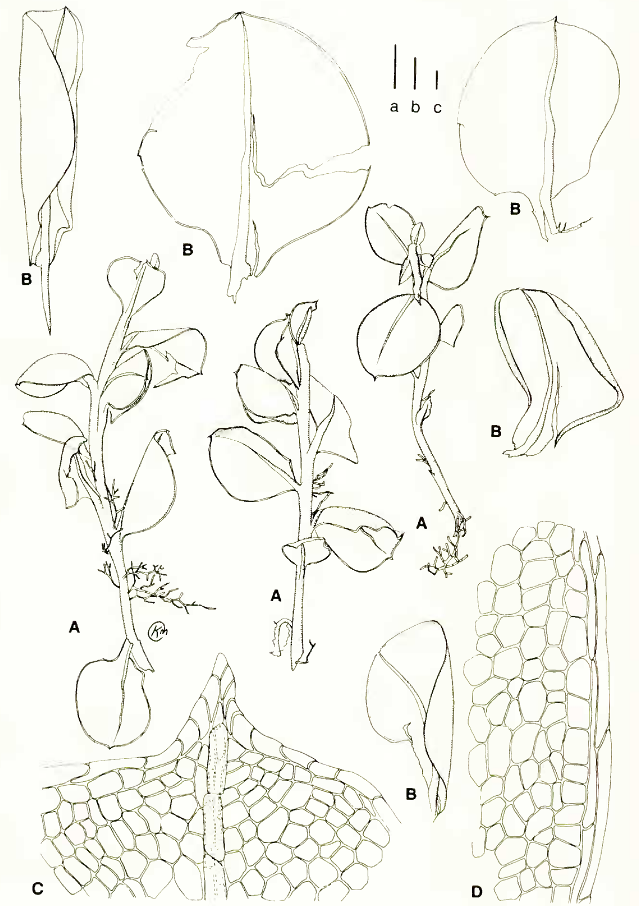

FIG. 3. Fossils of *Cinclidium latifolium* from the Clinton Power Station Site, De Witt Co., Illinois. A. Three plants (scale bar a). B. Five leaves from the same plant, note inrolled laminae in some leaves (b). C. Apex of leaf (c). D. Cells at edge of leaf (c). Scale bars: a = 1 mm, b = 0.5 mm, c = 10 μm. Drawings by Kathryn M. Conway.

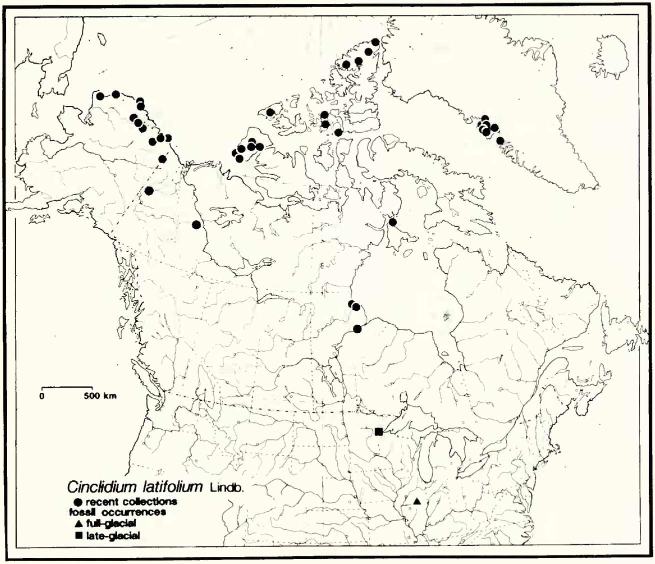

FIG. 4. Distribution of *Cinclidium latifolium* in North America. Map showing its present distribution and location of two late-Pleistocene fossil occurrences. Contemporary distribution based on map in Mogensen (1973), specimens examined, and information courtesy of G. S. Mogensen.

Ithaca, Tompkins County, New York (Miller and Schmidt, in prep.) produced abundant fossils of *Trichostomum arcticum,* a high-arctic species (Steere 1965; Schofield 1972), and other arctic-subarctic mosses, including *Hypnum bambergeri, Scorpidium turgescens, Timmia norvegica,* and at least 10 others. Leaves of the arctic-subarctic angiosperm *Dryas integrifolia* are abundant, and the pollen assemblage is dominated by sedge (77%), with pine (12%) and spruce (3%) subordinate. I have obtained the following AMS ages for two hardwood (*Salix?*) twigs from the organic bed: 27,000 ± 360 yr B.P. (Beta-27682, ETH-4474) and 33,940 ± 710 yr B.P. (Beta-32973, ETH-5699), indicating that the Sixmile Creek organic bed is 7,000 to 14,000 years older than the Illinois and Ohio full-glacial moss peats described here.

Current paleobotanical study in the North American Arctic has confirmed the antiquity of present members of the arctic flora such as *Cinclidium latifolium,* fossils of which are known from three Pliocene deposits, the Beaufort Formation of Prince Patrick and Meighen Islands and the Beaver Peat, west-central Ellesmere Island (Matthews and Ovenden 1990). Arctic mosses are also present in Plio-Pleistocene peats of Kap København, North Greenland (Mogensen 1984). These late Tertiary–early Quaternary paleobryofloras contain the remains of numerous mosses. The age of the Beaufort Formation on Meighen Island is ca. 3 Ma (million years) on the basis of geological and paleontological evidence (Matthews and

Ovenden 1990), while that of the Kap København formation is younger, 2.5–2.0 Ma (Bennike 1990). Scattered trees, *Picea mariana, Thuja occidentalis,* and *Larix groenlandii* (extinct), grew in places surrounded by open tundra vegetation in North Greenland at this time (Bennike and Böcher 1990), whereas the older (and more northern) Beaufort peats of Meighen Island contain spruce and pine macroremains together with fossils of tundra plants (Matthews and Ovenden 1990). It is possible that these late-Tertiary floras minus the trees, many of the shrubs, and the extinct species, would have been similar floristically to contemporary Arctic floras. Thus, many moss species of current arctic distribution have had a history of occurrence at high latitudes over millions of years.

The traditional interpretation has held that the present arctic flora assembled after the end of the Pleistocene through dispersal from unglaciated refugia in Beringia and parts of arctic and boreal Canada (Steere 1965). To this may now be added dispersal northward from areas just beyond or near the limit reached by the continental ice margin in central North America. The fate of populations of arctic species of mosses known to have occurred at low elevation in an area about 1000 km from east to west at the time the ice margin reached its maximum late-Wisconsinan extent, or some several thousands of years before this, will be discovered during studies of moss-rich sediments in the region between 40° North Latitude and the Arctic. Because fossils of arctic mosses have been found in younger sediments at places 750 km north of the midcontinent area (ca. 47° North), additional information should allow the role of a southern center of dispersal to be understood more fully.

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LITERATURE CITED

Baker, R. G., R. S. Rhodes II, D. P. Schwert, A. C. Ashworth, T. J. Frest, G. R. Hallberg and J. A. Janssens. 1986. A full-glacial biota from southeastern Iowa, USA. J. Quaternary Sci. 1: 91–107.

———, A. E. Sullivan, G. R. Hallberg and D.G. Horton, 1989. Vegetational changes in western Illinois during the onset of late Wisconsinan glaciation. Ecology 70: 1363–1376.

Bennike, O. 1990. The Kap København Formation: Stratigraphy and paleobotany of a Plio-Pleistocene sequence in Peary Land, North Greenland. Meddel. Grønland, Geosci. 23: 1–85 + 1 unpaged table.

——— and J. Böcher. 1990. Forest-tundra neighboring the North Pole: Plant and insect remains from the Plio-Pleistocene Kap København Formation, North Greenland. Arctic 43: 331–338.

Brassard, G. R. 1971. The mosses of northern Ellesmere Island, arctic Canada. II. Annotated list of the taxa. Bryologist 74: 282–311.

———. 1976. The mosses of northern Ellesmere Island, arctic Canada. III. New or additional records. Bryologist 79: 480–487.

Burns, G. W. 1958. Wisconsin age forests in western Ohio II. Vegetation and burial conditions. Ohio J. Sci. 58: 220–230.

Crum, H. 1972. The geographic origins of the mosses of North America's eastern deciduous forest. J. Hattori Bot. Lab. 35: 269–298.

Garry, C. E., D. P. Schwert, R. G. Baker, T. J, Kemmis, D. G. Horton and A. E. Sullivan. 1990. Plant and insect remains from the Wisconsinan interstadial/stadial transition at Wedron, north-central Illinois. Quaternary Res. 33: 387–399.

Goldthwait, R. P. 1958. Wisconsin age forests in western Ohio I. Age and glacial events. Ohio J. Sci. 58: 209–219.

Holmen, K. 1953. Bryophytes of Fosheim Pennisula, Ellesmere Island. Bryologist 56: 242–248.

Ireland, R. R., G. R. Brassard, W. B. Schofield and D. H. Vitt. 1987. Checklist of the mosses of Canada II. Lindbergia 13: 1–62.

Janssens, J. A. 1984. *Cinclidium latifolium* Lindb. in the late-glacial of northern Minnesota, USA. Lindbergia 10: 121, 122.

———. 1990. Bryophytes. *In:* B. G. Warner (ed.), *Methods in Quaternary Ecology.* Geoscience Canada Reprint Series 5: 23–36.

——— and R. G. Baker. 1984. A full-glacial bryophyte assemblage from southeastern Iowa, USA. J. Bryol. 13: 201–207.

Kapp, R. O. and A. M. Gooding. 1964. Pleistocene vegetational studies in the Whitewater Basin, southeastern Indiana. J. Geol. 73: 307–326.

King, F. B. 1979. Plant macrofossils from the Athens North Quarry. Illinois State Geol. Surv. Guidebook 13: 114, 115.

King, J. E. 1979. Pollen analysis of some Farmdalian and Woodfordian deposits, central Illinois. Illinois State Geol. Surv. Guidebook 13: 109–113.

Lowell, T., K. Savage, A. Dell, A. V. Morgan, J. Pilney, N. Miller and L. Shane. 1990a. Late Wisconsin glacial maximum biota, Cincinnati, Ohio. Canad. Quaternary Assoc. Amer. Quaternary Assoc. First Joint Meeting Program Abstr. Page 23. [Quaternary Sci. Inst., Univ. Waterloo, Canada.]

———, ———, C. S. Brockman and R. Stuckenrath. 1990b. Radiocarbon analyses from Cincinnati, Ohio, and their implications for glacial stratigraphic interpretations. Quaternary Res. 34: 1–11.

Martin, P. S. 1959. How many logs make a forest? Ohio J. Sci. 59: 221, 222.

Matthews, J. V., Jr. and L. E. Ovenden. 1990. Late Tertiary plant macrofossils from localities in arctic/subarctic North America: A review of the data. Arctic 43: 364–392.

Miller, N. G. 1976. Quaternary fossil bryophytes in North America: A synopsis of the record and some phytogeographic implications. J. Hattori Bot. Lab. 41: 73–85.

———. 1979. Paleoecological comments on fossil mosses in a buried organic bed near Peoria, Tazewell County, Illinois. Illinois State Geol. Surv. Guidebook 13: 116.

———. 1984. Tertiary and Quaternary fossils. *In:* R. M. Schuster (ed.), *New Manual of Bryology* 2: 1194–1232. Nichinan, Japan: Hattori Botanical Laboratory.

———. 1990. Plant macrofossils. *In:* A. V. Morgan (ed.), *Biological Techniques in Paleoenvironmental Interpretation.* Pages 30–72. Quaternary Sciences Institute. University of Waterloo. Waterloo, Ontario.

——— and S. T. Jackson. 1989. The setting and composition of full-glacial moss floras in the American Middle West. Am. J. Bot. 76(6): 12. [Abstract.]

Mogensen, G. S. 1973. A revision of the moss genus *Cinclidium* Sw. (Mniaceae Mitt.) Lindbergia 2: 49–80.

———. 1984. Pliocene or early Pleistocene mosses from Kap København, North Greenland. Lindbergia 10: 19–26.

Montagnes, R. J. S. 1990. The habitat and distribution of *Meesia triquetra* in North America and Greenland. Bryologist 93: 349–352.

Nyholm, E. 1954–1969. *Illustrated Moss Flora of Fennoscandia* II. Musci. Lund: CWK Gleerup.

Schofield, W. B. 1969. Phytogeography of northwestern North America: Bryophytes and vascular plants. Madroño 20: 155–207.

———. 1972. Bryology in arctic and boreal North America and Greenland. Canad. J. Bot. 50: 1111–1133.

——— and H. A. Crum. 1972. Disjunctions in bryophytes. Ann. Missouri Bot. Gard. 59: 174–202.

Schuster, R. M. 1983. Phytogeography of the Bryophyta. *In:* R. M. Schuster (ed.), *New Manual of Bryology* 1: 463–626. Nichinan, Japan: Hattori Botanical Laboratory.

Schwert, D. P. and A. C. Ashworth. 1988. Late Quaternary history of the northern beetle fauna of North America: A synthesis of fossil and distributional evidence. Mem. Entomol. Soc. Canada 144: 93–108.

Smith, A. J. E. 1978. *The Moss Flora of Britain and Ireland.* Cambridge and other cities: Cambridge University Press.

Steere, W. C. 1953. On the geographical distribution of arctic bryophytes. Publ. Stanford Univ. Biol. Sci. 11: 30–47.

———. 1965. The boreal bryophyte flora as affected by Quaternary glaciation. *In:* H. E. Wright, Jr. and D. G. Frey (eds.), *The Quaternary of the United States.* Pages 485–495. Princeton, New Jersey: Princeton University Press.

———. 1969. Asiatic elements in the bryophyte flora of western North America. Bryologist 72: 507–512.

———. 1978. The mosses of arctic Alaska. Bryophyt. Biblioth. 14: i–x, 1–508.

Vitt, D. H. 1975. A key and annotated synopsis of the mosses of the northern lowlands of Devon Island, N.W.T., Canada. Canad. J. Bot. 53: 2158–2197.

Wright, H. E., Jr. 1981. Vegetation east of the Rocky Mountains 18,000 years ago. Quaternary Res. 15: 113–125.